# ARE CROWN FIRES NECESSARY FOR TABLE MOUNTAIN PINE?

Thomas A. Waldrop
USDA Forest Service, Southern Research Station, 239 Lehotsky Hall, Clemson, SC 29634

Patrick H. Brose
USDA Forest Service, Northeastern Research Station, P.O. Box 267, Irvine, PA 16329

Nicole Turrill Welch
Department of Biology, Middle Tennessee State University, P.O Box 60, Murfreesboro, TN 37132

Helen H. Mohr
USDA Forest Service, Southern Research Station, 239 Lehotsky Hall, Clemson, SC 29634

Ellen A. Gray
Department of Forestry, Wildlife and Fisheries. University of Tennessee, Knoxville, TN 37901

Frank H. Tainter and Lisa E. Ellis
Department of Forest Resources, Clemson University, Clemson, SC 29634

## ABSTRACT

Ridgetop pine communities of the southern Appalachian Mountains have historically been maintained by lightning- and human-caused fires. Because of fire suppression for several decades. these stands are entering later seral stages. Such stands typically have an overstory of Table Mountain pine (*Pinus pungens*) that is being replaced by shade-tolerant chestnut oaks (*Quercus prinus*). The shrub layer consists of dense mountain laurel (*Kalmia latifolia*). Previous research suggests that restoration of these communities can be accomplished with high-intensity fires that open the forest canopy and expose mineral soil. Three recent studies examined plant-community response to high-intensity prescribed fires. A series of four supporting studies helps to explain some of the results of these field studies. High- and medium-high-intensity fires provided adequate sunlight for pine seedlings. whereas medium-low- and low-intensity fires did not. Post-burn duff was deep (<5 cm) and did not vary by fire intensity. We observed sufficient seedling densities to restore pine-dominated stands (<9.000/ha) after all but the highest intensity fires. Many seedlings survived the first growing season as their roots penetrated duff to reach mineral soil. Hardwood rootstocks resprouted on sites treated with all fire intensities and may out-compete pine seedlings. High-intensity fires may have reduced mycorrhizal abundance and moisture availability for new germinants. Fires of lower intensity than previously recommended or multiple fires of very low intensity may provide the best conditions for pine regeneration.

*keywords:* Appalachian Mountains, fire-dependent communities. *Pinus pungens,* prescribed fire, regeneration, stand-replacement fire, Table Mountain pine.

## INTRODUCTION

The southern Appalachian Mountains have long been appreciated for their diversity of plants and plant communities. Many factors have been responsible for establishing and maintaining this diversity. including a mosaic of soils, aspects, elevations. weather patterns. and disturbance regimes. However, a key factor for several communities has been missing for several decades: large-scale fire. Lightning- and human-caused fires have played a significant role in the evolution of southern Appalachian plants and plant communities

(Van Lear and Waldrop 1989). Fire suppression policies on public lands have likely reduced the diversity of the southern Appalachian Mountains and may threaten the existence of some plants and communities.

A species of concern is Table Mountain pine. This shade-intolerant Appalachian endemic occurs from central Pennsylvania to northeastern Georgia. It is found on thin, dry soils with southern and western aspects, and at elevations of 300 to 1,200 m (Zobel 1969). Serotinous cones, which are found in the species throughout its range, suggest that fire is needed to regenerate Table Mountain pine. Microsite conditions

needed for seedling establishment, such as high levels of sunlight and little or no litter or duff, are similar to those created by high-intensity fire. Sutherland et al. (1995) found a Table Mountain pine community in Virginia that was maintained by major fires occurring approximately every 10 years until the 1940s, which was probably when fire suppression efforts became successful in the area.

Stands in which Table Mountain pines occur throughout the region are entering late seral stages. Such stands are often dominated by oaks, particularly chestnut oak and hickories (*Carya* spp.) (Zobel 1969, Turrill et al. 1997). This pattern indicates that the short-lived, shade-intolerant pines will be replaced by the longer-lived, shade-tolerant hardwoods if some form of regeneration, such as stand-replacement fire, does not occur. As a result of changing species dominance and stand structure, Table Mountain pine woodlands are recognized by the Southern Appalachian Assessment as one of 31 rare communities in the southern Appalachian Mountains (SAMAB 1996).

Most research on the role of fire in Table Mountain pine stands has been limited to post-wildfire studies, which suggest that high-intensity prescribed fires are needed to remove the forest canopy and expose mineral soil for successful regeneration. Zobel (1969) found that serotinous cones opened in lightly burned areas, but that seedlings survived only where fires killed overstory trees and erosion exposed mineral soil. Likewise, Sanders (1992) observed the greatest proportion of Table Mountain pine seedlings in high- and moderate-intensity burn areas, where the canopy was open and mineral soil exposed. Williams and Johnson (1992) found that seeds were abundant on the ground in lightly disturbed stands where no fire occurred. However, seedlings were successful only on microsites with thin litter layers (<4 cm) and where the canopy was more open than in surrounding stands. Such microsites usually were created by ice storms (Williams 1998).

Williams (1998) suggested that Table Mountain pine stands are in decline as a result of fire suppression and inadequate understanding of the species regeneration biology. The need to use high-intensity, stand-replacement prescribed burning is suggested by the combination of serotinous cones, shade-intolerant seedlings, and requirement of bare soil for germination. However, accomplishing these burns is difficult. Such prescriptions create a narrow window of opportunity and raise questions about worker safety and smoke management. To date, only three studies have conducted prescribed burns to better understand the conditions necessary for Table Mountain pine regeneration. Together, these three studies examine community response to varying degrees of fire intensity, as well as seedling establishment in various microhabitats. This paper examines the results of the three prescribed fire studies (Turrill 1998, Waldrop and Brose 1999, and one study presented here) and four supporting studies (presented here) of regeneration ecology to evaluate the need for high-intensity, stand-replacement fires for regenerating Table Mountain pine.

# CURRENT RESEARCH ON STAND-REPLACEMENT PRESCRIBED BURNING

Stand-replacement prescribed burning has been studied at three separate burn units in the southern Appalachian Mountains: the Grandfather Ranger District, Pisgah National Forest, North Carolina; the Tallulah Ranger District, Chattahoochee National Forest, Georgia; and a burn unit in South Carolina managed by both the Andrew Pickens Ranger District, Sumter National Forest, and the Buzzard's Roost Preserve of the South Carolina Heritage Trust Program. In this paper, these burn units will be referred to as the Grandfather, Tallulah, and Buzzard's Roost burns, respectively. The Grandfather burn was previously described by Turrill (1998) and Welch et al. (2000). The Tallulah burn was described by Waldrop and Brose (1999). The burns conducted for all three studies varied in their effects on opening the forest canopy and removing litter and duff. Comparisons of these field studies allow an evaluation of the amount of Table Mountain pine regeneration under natural conditions.

Several supporting studies provide insight to disturbance history and methods of evaluating stands for their potential of regeneration success. Waldrop et al. (1999) conducted a greenhouse study to evaluate the effects of shade and duff on seedling establishment. Ongoing studies include the dendrochronology of ridgetop pine stands across the southern Appalachians, seed biology of Table Mountain pine, and mycorrhizal associations in burned Table Mountain pine stands. We discuss the preliminary results of each study.

## Fire Intensity and Stand Replacement of Table Mountain Pine

The Tallulah burn occurred on the War Woman Wildlife Management Area of the Tallulah Ranger District, Chattahoochee National Forest in northern Georgia. Prior to burning, mean total basal area in study stands was 28.2 m²/ha. Hardwoods composed 22.7 m² of this total and pines the remaining 5.5 m². Chestnut oak was the predominant hardwood and almost all pines were Table Mountain pine. USDA Forest Service personnel conducted a stand-replacement prescribed fire on a 345-ha unit in April 1997. The burn area included sharp ridgetops and steep slopes with northeastern or southwestern aspects. The fire was ignited by hand and by helicopter to create a ring fire that reached greatest intensity within ridgetop Table Mountain pine stands. Fire intensity ranged from subcanopy ground fires to crown fires carrying from tree to tree. The Tallulah burn was sufficiently large and its intensity was sufficiently variable to allow comparisons of regeneration success among areas burned at different intensities (Waldrop and Brose 1999).

The Buzzard's Roost Burn occurred on a tract consisting of approximately 100 ha managed by the South Carolina Heritage Trust Program and 45 ha managed by the Andrew Pickens Ranger District, Sumter National Forest. Prior to burning, mean total basal area

Table 1. Characteristics of Table Mountain pine stands in the southern Appalachian Mountains during the year following stand-replacement prescribed burning.

| Variable | Fire | Fire intensity | | | |
|---|---|---|---|---|---|
| | | Low | Medium-Low | Medium-High | High |
| Pine basal area (m²/ha) | Tallulah[a] | 5.9 | 6.0 | 1.1 | 0.0 |
| | Buzzard's Roost[b] | 8.4 | 6.4 | 0.0 | |
| | Grandfather[c] | | 21.6 | | |
| Hardwood basal area (m²/ha) | Tallulah | 16.8 | 5.1 | 0.5 | 1.0 |
| | Buzzard's Roost | 11.8 | 4.2 | 7.6 | |
| | Grandfather | | 4.3 | | |
| Total basal area (m²/ha) | Tallulah | 22.7 | 11.1 | 1.6 | 1.0 |
| | Buzzard's Roost | 19.2 | 10.8 | 7.6 | |
| | Grandfather | | 25.9 | | |
| Hardwood sprouts (no./ha) | Tallulah | 32,150 | 37,371 | 26,590 | 31,537 |
| | Buzzard's Roost | 20,553 | 25,582 | 17,505 | |
| | Grandfather | | 2,295 | | |
| Pine seedlings (no./ha) | Tallulah | 13,852 | 22,551 | 9,016 | 3,448 |
| | Buzzard's Roost | 551 | 995 | 961 | |
| | Grandfather | | 7,699 | | |

[a] Tallulah Ranger District, Chattahoochee National Forest, Georgia (Waldrop and Brose 1999). Prescribed fire in April 1997.
[b] Andrew Pickens Ranger District, Sumter National Forest, and Buzzard's Roost Preserve, South Carolina Heritage Trust, South Carolina. Prescribed fire on 4 March 1998.
[c] Grandfather Ranger District, Pisgah National Forest, North Carolina (Welch et al. 2000). Prescribed fire in May 1996.

in study stands was 21.0 m²/ha. Hardwoods made up 10.9 m² of this total and pines the remaining 10.1 m². Chestnut oak was the predominant hardwood and almost all pines were Table Mountain pine. Personnel of the USDA Forest Service, South Carolina Department of Natural Resources, and the South Carolina Forestry Commission conducted the burn on 4 March 1998. The exterior of the unit was hand-fired to widen fire lines. Aerial ignition, using a plastic sphere dispenser, began midway up each of two south-facing slopes to produce crown fires along ridge tops. Fire intensity ranged from subcanopy ground fires to flame lengths reaching the lower levels of the stand canopy.

The Grandfather burn was a 3-ha prescribed fire on the Grandfather Ranger District, Pisgah National Forest. Mean total basal area was 32.3 m²/ha prior to the burn. Hardwoods composed 8.7 m²/ha, and pines 23.6 m²/ha. Blackgum (*Nyssa sylvatica*) was the predominant hardwood. The pine component was 51% Table Mountain pine, 39% pitch pine (*P. rigida*), and 10% Virginia pine (*P. virginiana*). USDA Forest Service crews used a combined ring and head fire technique to burn the stand in May 1996. Flames reached to lower limbs on most trees and entered the canopy on a small portion of the stand.

The prescriptions applied in these studies produced four fire intensities defined by Waldrop and Brose (1999): low, medium-low, medium-high, and high. All intensities were observed in the Tallulah burn and all but high intensity was observed in the Buzzard's Roost burn. At the Grandfather burn, only the medium-low intensity was observed. Waldrop and Brose (1999) gave a detailed description of how discriminant functions were used to classify fire intensity. Intensity categories generally can be described as follows: 1) Flames of low-intensity fires never reached into the crown of trees and uniformly burned the area. 2) Medium-low-intensity fires had flames slightly taller than those of low-intensity fires; they burned less

uniformly and produced hot spots where flames reached into crowns and killed large trees. 3) Flames of medium-high-intensity fires typically reached into the crowns of all overstory trees. 4) Flames of high-intensity fires generally exceeded the crowns of overstory trees and carried from crown to crown.

High-intensity fires occurred only in the Tallulah burn where they killed nearly all overstory trees, leaving only 1.0 m² of basal area/ha (Table 1). Medium-high-intensity fires occurred at Tallulah and Buzzard's Roost. These fires were also effective at killing overstory trees, leaving only 1.6 and 7.6 m²/ha of basal area, respectively. Mortality was high across all diameter size classes following both high- and medium-high-intensity fires. Sunlight reaching the forest floor may have been adequate for seedling survival following fires of both intensities. High- and medium-high-intensity fires were the only ones of sufficient intensity to kill enough of the overstory to achieve conditions of stand replacement.

Medium-low- and low-intensity fires reduced canopy cover (Table 1), but residual basal area may have been too high in all three studies to allow stand replacement. Medium-low-intensity fires reduced basal area to 11.1 m²/ha at the Tallulah burn and 10.8 m²/ha at the Buzzard's Roost burn, but left 25.9 m²/ha at the Grandfather burn. Low-intensity fires had little effect on basal area, leaving 22.7m²/ha at the Tallulah burn and 19.2 m² at the Buzzard's Roost burn. Mortality was greatest in lower diameter at breast height (dbh) classes (<15 cm dbh) following fires of medium-low and low intensity. Shade from surviving trees after low- and medium-low-intensity fires may prevent pine seedling survival.

Prolific hardwood sprouting was observed following fires of all intensities (Table 1). Generally, under all fire intensities there were >20,000 stems/ha 1 year after burning, and they were growing rapidly (>1 m tall after 1 growing season). Competition from these

sprouts may eliminate any pine regeneration after a fire of any intensity. This result suggests that multiple low-intensity fires may be necessary to reduce hardwood abundance while maintaining a seed source among large pines.

Post-burn counts of Table Mountain pine seedlings in the Tallulah and Grandfather burns suggest that fires were of sufficient intensity to open serotinous cones throughout burn units, even in areas burned at low intensity. Post-burn pine density ranged from 3,448 to >22,500 stems/ha (Table 1) in these two units. An unexpected result was that the lowest pine densities in the Tallulah burn were in areas burned at the highest intensity. This suggests that cones were consumed or seeds killed by intense heat, or that the seedbed became less suitable due to excessive exposure to sunlight and evaporation.

Although plots in high-intensity burn areas had fewer seedlings, if they were well dispersed, the 3,448 seedlings/ha present in those areas should create pine-dominated stands. However, Table Mountain pine seedlings were found at only 51% of the sampling points, indicating that portions of burned areas had no pine regeneration. Hardwoods will likely dominate such areas. Plots in areas burned at medium-high intensity also indicated low pine stocking (64%). If seedlings receive sufficient sunlight, pine density and stocking levels in those areas burned at low and medium-low intensities should be sufficient to create pine-dominated stands.

Table Mountain pine regeneration was poor at all fire intensities observed in the Buzzard's Roost burn. Poor regeneration success could be caused by a number of factors including thick residual duff or lack of viable seed. Duff layers after burning at Buzzard's Roost averaged only 4.4 cm deep and did not vary by fire intensity. Duff remaining after the Tallulah burn was generally deeper with 5.3, 3.8, 6.4, and 6.6 cm for the low-, medium-low-, medium-high-, and high-intensity fires, respectively. The percentage of seedlings with roots penetrating mineral soil at Tallulah was 71.1, 94.6, 63.0, and 56.1 for the same order of fire intensities (Waldrop and Brose 1999). Welch et al. (2000) observed pine regeneration on approximately 9.1 cm of combined litter and duff after the Grandfather burn. Successful regeneration of Table Mountain pine on the thicker duff layers found in the Tallulah and Grandfather burns may indicate that low regeneration counts at the Buzzard's Roost burn are a result of lower availability of viable seed. Methods for estimating seed viability prior to burning are currently unavailable for Table Mountain pine stands.

Supporting Studies

### Seed Biology

In the past, studies of prescribed burning assumed an adequate seed source that did not vary among stands or stand conditions. Any regeneration failures could have been caused by an inadequate seed source. A study by Gray et al. (2002) helps to identify stands

Table 2.  Percent viability of Table Mountain pine seed by tree age and cone age within a tree, southern Appalachian Mountains.

| Tree age class (years) | Cone age | | | | |
|---|---|---|---|---|---|
| | 2 years | 3 years | 4 years | 5 years | All ages |
| 5–10 | 8 | 23 | 1 | — | — |
| 11–25 | 20 | 32 | 41 | 23 | 27 |
| 26–50 | 33 | 11 | 24 | 56 | 31 |
| 51–75 | 29 | 20 | 34 | 36 | 30 |
| 75+ | 29 | 13 | 54 | 39 | 33 |
| All tree age classes | 24 | 21 | 34 | 36 | |

that have an adequate seed source for regeneration. This study will help managers determine the abundance and viability of seed from a range of tree ages, as well as from cones of different ages. Results indicate that seed viability was moderate, generally between 20% and 50%, from cones of all ages and from trees older than 10 years (Table 2). Viability did not appear to vary by age after trees reached 10 years. However, viability seemed to increase as cones matured to 4 or 5 years old. These results indicate that, if cone numbers are adequate, stands over a wide range of ages may be considered as candidates for burning. A surprising result is the presence of cones with viable seed on young trees. Trees within the 5- to 10-year age class had 3-year-old cones with 23% seed viability. This result suggests that Table Mountain pines are adapted to regenerating under regimes of low-intensity fires, which may occur every 5 to 10 years. These results also indicate that if frequent low-intensity fires are used, that viable seed will become available every 2 to 3 years as long as fires do not kill overstory pines.

### Seedbed Habitat

In order to assess seedling establishment, Waldrop et al. (1999) conducted a greenhouse study that used shade and duff treatment combinations similar to those observed in the field. Duff categories included depths of 0, 5, and 10 cm; and shade levels included 0%, 30%, 63%, and 85% shade. Table Mountain pine seeds were collected on the Chattahoochee National Forest, adjacent to the Tallulah burn. Soil and duff were collected from the Buzzard's Roost burn unit soon after burning. Seeds were germinated and allowed to grow under these conditions for 3 months. We compared survival of seedlings grown in the greenhouse to field seedling survival in the burn described by Waldrop and Brose (1999).

Stem density typically was greater in 5-cm duff than in bare soil or 10-cm duff (Figure 1). This pattern remained constant for all shade categories except the 0%-shade category. In 0% shade, stem densities in pots with 5-cm duff were equal to stem densities in pots without duff. Without shade, the mulching effect of a 5-cm duff layer may not have been adequate to prevent moisture deficit and seedling death.

Lack of shade reduced seed germination and the survival of germinants, while heavy shade reduced survival; more seedlings become established under 30% shade than under full light or the higher shade
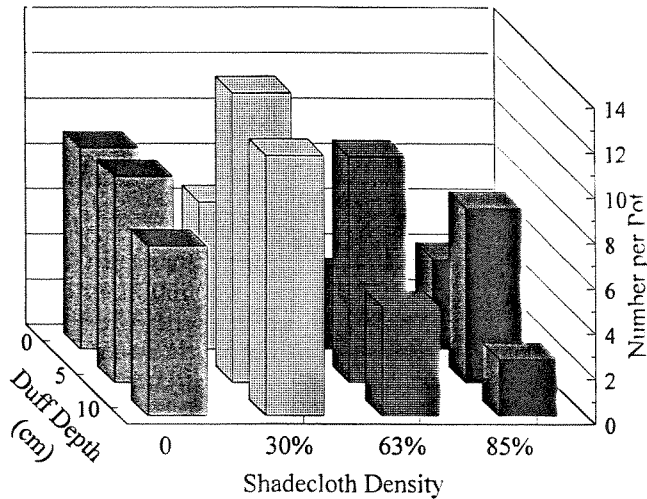
Fig. 1.   Table Mountain pine seedling density per pot after a 90-day greenhouse study to assess seedling establishment for all combinations of shade level and duff depth.
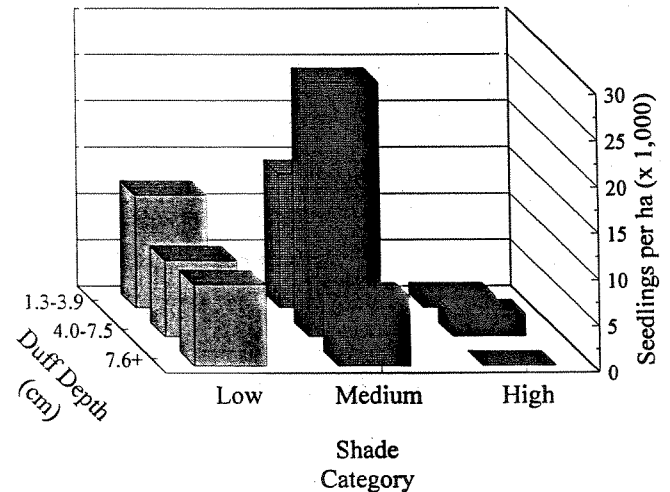


Fig. 2.   Table Mountain pine seedling density in the Tallulah (Tallulah Ranger District, Chattahoochee National Forest, Georgia) and Buzzard's Roost (Andrew Pickens Ranger District, Sumter National Forest, South Carolina, and Buzzard's Roost Preserve, South Carolina Heritage Trust) burn units at the end of one growing season for all combinations of shade and duff depth categories.

levels. This pattern was constant among pots with 5- and 10-cm duff but differed among pots with no duff (Figure 1). With no duff, fewer seedlings/pot occurred under 30% shade than under no shade, although this difference was not significant. Without the mulching effect of duff, 30% shade may not be adequate to prevent moisture deficit.

If germination and survival in the field follow the same patterns as in the greenhouse, these data provide a partial description of seedbed conditions necessary to establish Table Mountain pine. Because of differences in study designs, field results shown here do not provide a direct comparison to greenhouse results. However, results of the two studies are similar. In the field, stem numbers did not vary significantly at different duff depths within a shade category (Figure 2). Seedling numbers were not significantly different between low- and medium-shade categories, but both had significantly more stems than did the high-shade category. Under high shade, stem density was <2,500 seedlings/ha at all duff depths, probably too few to adequately regenerate a stand. Stem numbers in medium and low shade ranged from 7,470/ha for medium shade with >7.5 cm of duff to >27,000 stems/ha under medium shade and 4.0 to 7.5 cm of duff. Each of these stem densities probably exceeds the minimum needed to regenerate the stand.

The moderate levels of shade and duff that this study suggests are optimum seedbed habitat differ somewhat from previous recommendations. Although the exact fire regimes necessary to create this type of habitat are unknown, these results do not suggest that a single high-intensity fire is mandatory. Multiple lower-intensity fires could maintain an overstory and seed source while reducing the duff without exposing mineral soil.

### Fire Intensity and Mycorrhizae

The need for mycorrhizae is generally accepted for southern pine seedlings grown in nurseries, but it has

not been studied for non-timber species such as Table Mountain pine. Both ectomycorrhizae and vesicular–arbuscular mycorrhizae may be necessary for survival of Table Mountain pine seedlings, but their respective roles in Table Mountain pine regeneration and their responses to high-intensity fires have not been considered. Neary et al. (2000) suggested that fire intensity strongly affects the degree and duration of reduced soil microbial activity. Neary et al. (2000) also suggested that after a period of low activity, microbial populations increase in areas burned at high intensity to a level much higher than in unburned areas, or in areas burned at low intensity. This pattern may suggest that Table Mountain pine seedlings will not develop for some time after high-intensity burning, but that they may eventually benefit from increased microbial populations. If so, prescribed burns should be conducted far enough in advance of spring germination to allow these populations to recover.

Ellis et al. (2002) examined the relationship of fire intensity to mycorrhizal development on Table Mountain pine roots. One- and two-year-old seedlings were collected on plots established after the Tallulah burn (Waldrop and Brose 1999). Seedling root biomass was quantified; ectomycorrhizal root tips were characterized; and ectomycorrhizal root tip presence was compared by seedling age and fire intensity. In a laboratory examination, ectomycorrhizal root tip formation was compared among seedlings grown in media exposed to a range of temperatures that could be found in a prescribed burn.

Results indicates that *Pisolithus tinctorius, Suillus granulatus,* and *Cenococcum* spp. are the predominant symbionts that form mycorrhizal root tips in Table Mountain pine stands. Two years after burning, seedlings growing in areas burned at medium-low and medium-high fire intensities had twice as many mycor-
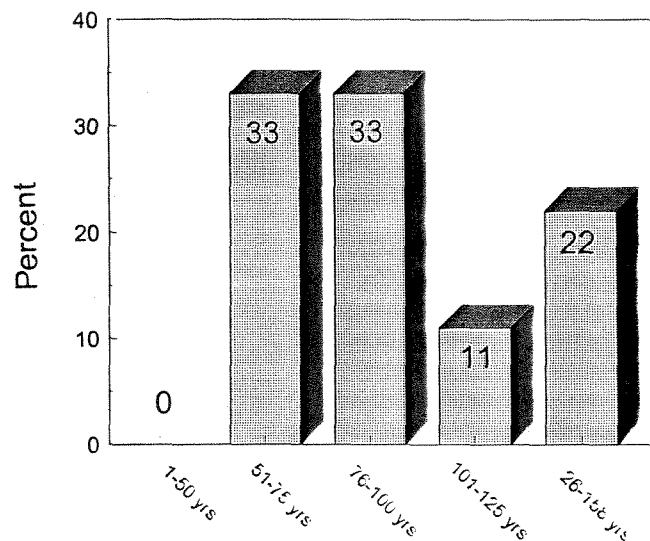
Fig. 3. Age distribution of Table Mountain pines sampled in 1999 in two burn units on the Tallulah Ranger District, Chatta-hoochee National Forest, Georgia.

rhizal root tips (40%) than seedlings from sites burned at high intensities (22%), indicating a lasting negative impact of high-intensity prescribed fires. Laboratory results were similar, showing that mycorrhizal root tips are less common after fungi have been exposed to temperatures over 50 °C and almost absent after exposure to temperatures up to 80 °C. These results suggest that poor regeneration of Table Mountain pine in the Tallulah burn after high-intensity burning could have been caused by poor formation of mycorrhizal root tips. Frequent low-intensity burning could be one means of avoiding loss of mycorrhizal fungi.

*Dendrochronology*

Little is known about the disturbance history of Table Mountain pine stands. The species may have been maintained by frequent low- to medium-intensity fires, infrequent high-intensity stand-replacing fires, or a combination of both. The dendrochronology study by Sutherland et al. (1995) provides valuable insight to fire frequency and stand dynamics for one Virginia site. A similar study was done by Brose et al. (2002) on the Tallulah, Buzzard's Roost, and other study sites. Cores were extracted from overstory trees and understory trees and shrubs in two burn units in Georgia, two in South Carolina, and one in Tennessee.

A preliminary analysis of stand dynamics in the two Georgia units suggests a history of frequent disturbance that lasted until the 1950s (Figure 3). Pines in the dominant canopy position are between 100 and 158 years old. However, numerous smaller pines are between 50 and 100 years old. Shrubs, particularly mountain laurel, are <50 years old, and there are no pines younger than 50 years. The frequency pattern of pine age classes indicates that pines were regenerating from the 1850s through the 1950s, and that these stands were relatively open. Well-established fire suppression policies in the 1950s allowed the shrub layer to become dominant and prevent continuing pine re-

generation. Successful restoration of these stands cannot be expected with a single prescribed burn of any intensity. Multiple burns or other control methods will be required to remove shrubs and competing hardwoods.

## CONCLUSIONS

The three studies described here represent the first attempts to restore ridgetop pine communities in the southern Appalachian Mountains with prescribed stand-replacement fires. Such fires have been attractive for a number of reasons: they provide a means of killing overstory trees and opening the forest floor to direct sunlight; they provide the heat needed to open serotinous cones; and they reduce thick duff layers or expose mineral soil. However, none of the fires observed in these studies should be considered successful for replacing older stands of mixed pines and hardwoods with newly regenerated stands of pines. Low-intensity fires at Tallulah and Buzzard's Roost and medium-low-intensity fires observed in all three burn units failed to kill more than a few overstory trees. High-intensity fires in one burn unit killed most overstory trees but resulted in few pine seedlings. Medium-high fires provided abundant overstory mortality and pine regeneration. However, fires of all intensities failed to control competition from hardwood and shrub sprouts.

Competition and shading from hardwoods and shrubs that sprout after burning may inhibit the development of a pine-dominated stand. Post-fire sprouting occurred more frequently in hardwood tree species (red maple [*Acer rubrum*], chestnut oak, and scarlet oak [*Quercus coccinea*]) than in shrub species (mountain laurel). The ability of Table Mountain pine seedlings to compete with the regeneration of other species is unknown. Frequent burning may be necessary to reduce hardwood sprout vigor.

The support studies presented here provide indirect evidence that ridgetop pine communities may be restored by frequent burning. The dendrochronology study shows that pines in study stands were uneven-aged and had regenerated frequently until the time of fire exclusion. The seed biology study suggests that a viable seed source is present over a wide range of tree ages and in cones that have been on trees for up to 5 years. This study also shows that very young trees produce viable seed, suggesting an adaptation to frequent burning. Studies of seedbed habitat and mycorrhizal populations provide evidence that the severe conditions produced by high-intensity burning are not necessary and may be detrimental to regeneration. Moisture may be limited due to lack of mycorrhizal tips on roots, loss of a mulching effect from the duff, and direct sunlight reaching the forest floor. Moderate levels of shade with some duff present were optimum for seedling survival, both in the greenhouse and in the field. These conditions may have been common in pre-1950s stands that burned often. Thick duff was a barrier to seedling development in all field studies but seedling roots can penetrate duff up to 7.5 cm thick.

The results presented here suggest that ridgetop pine stands were created by lower-intensity fires than once were thought necessary, and that such fires would aid in community restoration. Low-intensity prescribed fires, which can be used when the lower layers of the forest floor are moist, are less dangerous and present a larger window of opportunity than high-intensity fires. Low-intensity fires also decrease erosion potential on steep slopes and loss of site productivity.

There is still much to learn about restoring ridgetop pine stands. If seedlings continue to survive among sprout competition, a single medium-high-intensity fire may prove sufficient. However, these results were drawn from studies that tracked seedling survival and overstory mortality for only one growing season. The competitive ability of Table Mountain pine in young stands is unknown. Additional research also is needed to test fires in other seasons and multiple low-intensity burns. Such fires should be conducted so as to control hardwood and shrub sprouting while maintaining healthy overstory pines as a seed source. Physical, chemical, and biological properties of soils in ridgetop stands are likely to be affected by regeneration burns. These properties may affect seedbed conditions but they have not been studied. Finally, natural disturbances other than fire may have played an historical role in perpetuating this species; therefore, alternative management strategies, such as herbicides, may also improve Table Mountain pine regeneration.

## ACKNOWLEDGMENTS

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